

MAMMALIAN SPECIES No. 369, pp. 1–4, 3 figs.

Dipodomys compactus. By George D. Baumgardner

Published 12 April 1991 by The American Society of Mammalogists

Dipodomys compactus True, 1889

Gulf Coast Kangaroo Rat

Dipodomys compactus True, 1889:160. Type locality "Padre Island, [Cameron Co.] Texas" (Poole and Schantz, 1942).

Dipodops sennetti Allen, 1891:226. Type locality "near Brownsville, Cameron Co., Texas." Modified following Bailey (1905) to "Santa Rosa, 85 mi SW Corpus Christi" (Setzer, 1949). Refined to "Santa Rosa, near Sarita, Kenedy Co., Texas" by Baumgardner (1989).

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Dipodomyninae. This species contains two subspecies (Baumgardner and Schmidly, 1981):

D. c. compactus True, 1889:160, see above (*parvabullatus* Hall and *lagus* Hall are synonyms; Baumgardner and Schmidly, 1981).

D. c. sennetti (Allen, 1891:226), see above.

DIAGNOSIS. The Gulf coast kangaroo rat (Fig. 1) is of medium size and has five toes on each hind foot. The only similar kangaroo rat to occur in proximity to *D. compactus* is *D. ordii*. Externally, *D. compactus* differs from *D. ordii* in southern Texas by having a shorter tail. The tail of *D. compactus* is not crested, and its ventral pencil is lighter in color and more broken than in *D. ordii*, and does not extend to the end of the tail. The pelage of *D. compactus* is shorter, coarser, and, in areas of proximity to *D. ordii*, has an orangish cast, whereas that of the latter tends toward brownish hues (Baumgardner and Schmidly, 1981). Cranially, *D. compactus* is smaller than *D. ordii* from southern Texas as reflected primarily in the former having a shorter skull and narrower, less inflated mastoid bullae (Baumgardner and Schmidly, 1981; Schmidly and Hendricks, 1976). The supraoccipital and interparietal elements of *D. compactus* are wide with the interparietal rectangular to roundish (shown in Fig. 2.1 of Schmidly and Hendricks, 1976). The interparietal of *D. ordii* in southern Texas (shown in Figs. 2.2 and 2.3 of Schmidly and Hendricks, 1976) is more acutely pointed posteriorly and is more triangular (Baumgardner and Schmidly, 1981). Also, the species can be separated by karyotypes; *D. compactus* has a diploid number (2n) of 74 and number of autosomal arms (fn) of 144, whereas *D. ordii* has a 2n of 72 and an fn of 140 (Schmidly and Hendricks, 1976).

GENERAL CHARACTERS. Distinct gray (cartridge buff) and red (light ochraceous-buff) color phases of dorsal pelage occur in populations of *D. c. compactus*. In both phases the dorsal color covers the entire back and is purest on the sides and flanks with the upper parts lightly washed with black. The cheeks of both phases are white and their pinnae, plantar surfaces of their feet, and dorsal and ventral tail stripes are brownish (Setzer, 1949). The pelage color of both phases is lighter than that of other kangaroo rats in Texas and the pale ashy gray of the lighter phase is unique (Bailey, 1905). Proportion of gray specimens varies markedly in samples: Mustang Island, 17.2%; North Padre Island, 65.3%; South Padre Island, 93.3%; and Tamaulipas 5.6% (Baumgardner and Schmidly, 1981). Color of the dorsal pelage of specimens from the type locality of the mainland form (*D. c. sennetti*) is yellowish, ochraceous-buff mixed with black. The dark tint prevails over the mid-dorsal region from the crown to the base of the tail but lessens on the sides becoming almost purely buffy yellow on the flanks. The upper tail stripe is dusky brown with the lower stripe paler (Allen, 1891).

Coefficients of variation for external and cranial characters of adults from Mustang Island (Schmidly and Hendricks, 1976) ranged from 3.58 (length of hind foot, male) to 7.64 (length of body, female) and from 1.25 (greatest width of skull, female) to 9.99 (supraoccipital width, male), respectively. Most large coefficients of variation were

from males. A sample from the mainland of southern Texas had values ranging from 1.82 (length of hind foot, male) to 5.49 (total length, male) for external measurements and from 1.34 (greatest length of skull, female) to 15.32 (interparietal width, male) for cranial characters (Baumgardner and Schmidly, 1981).

Few characters exhibit statistically significant differences between the sexes of *D. compactus*. In general, however, males are slightly larger than females in external measurements, but smaller in most cranial ones (Baumgardner and Schmidly, 1981; Schmidly and Hendricks, 1976).

Means (in mm) of measurements for samples of males from mainland and island populations ranged as follows: total length, 216–230; length of tail, 111–126; length of hind foot, 35.8–37.7; greatest length of skull, 36.3–37.2; greatest breadth across bullae, 21.5–23.4; breadth across maxillary arches, 19.2–20.1; width of rostrum, 3.6–4.0; length of nasals, 13.6–14.0; least interorbital width, 12.1–13.1; and basilar length, 23.0–24.2 (Hall, 1951). Body masses (in g) of two males were 47 and 60 and of two females were 46 and 44 (Selander et al., 1962).

Dipodomys c. compactus from southern Padre Island are largest, whereas those from the Tamaulipan islands are smallest; Mustang Island samples are intermediate in size. Among mainland samples (*D. c. sennetti*), size increased slightly from east to west. Characters useful in distinguishing the subspecies were length of tail, length of hind foot, greatest length of skull, length of mastoid bullae, width of mastoid bullae, and depth of skull (Baumgardner and Schmidly, 1981).

DISTRIBUTION. *Dipodomys compactus* ranges primarily over southern Texas (Fig. 2). This species inhabits Mustang and Padre islands, Texas (Setzer, 1949), the barrier islands of Tamaulipas, Mexico (Hall, 1951), and the eastern two-thirds of the southern Texas mainland (Baumgardner and Schmidly, 1981).

FOSSIL RECORD. There are no fossil specimens of this taxon. Based on the degree of grooving on the sides of the cheek teeth and incidence of interruption of the enamel ring on the occlusal surface, *D. compactus* is regarded as the most primitive living species of kangaroo rats (Hibbard, 1954; Wood, 1935; Zakrzewski, 1981). Development of the dorsal portion of the auditory bullae of this species is equivalent to that of *Eodipodomys celtiservator* from the late Clarendonian age (Voorhies, 1975). Because of the arrangement of its auditory region and general proportions, Wood (1935) considered it similar to *Cupidinimus* and possibly descended from *D. minor* of the Upper Pliocene.



FIG. 1. A *Dipodomys compactus compactus* from Padre Island, Texas. Photograph by J. L. Tveten.

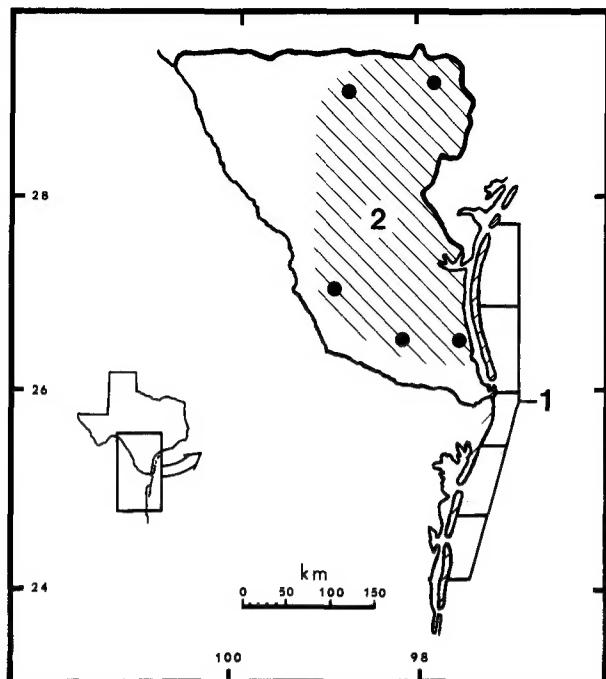


FIG. 2. Geographic distribution of the subspecies of *Dipodomys compactus*: 1, *D. c. compactus*; 2, *D. c. sennetti*. The northern boundary of the Rio Grande plain is depicted as a broad line along the northern and eastern edge of the area. Mainland marginal records beginning in the northeast are as follows: 2 mi. N Nixon, Gonzales Co. (Raun, 1959); WSW to 7 mi. E Lytle, Atascosa Co. (Blair, 1952); SSW to 2 mi. NE Bustamante, Zapata Co.; ESE to 4.4 mi. N Linn, Hidalgo Co. (Baumgardner and Schmidly, 1981); E to Sauz Ranch, Willacy Co. (Schmidly and Hendricks, 1976).

FORM. The skull is small and rectangularly shaped (Fig. 3) with the greatest breadth across the bullae only slightly greater than breadth across the zygomatic processes of the maxillae (Setzer, 1949). The mastoid bullae are relatively small for the genus (Hall, 1951; Wood, 1935). The interparietal element is wide for the genus (Wood, 1935) and is quadrate shaped, slightly hollow on its lateral margins, and with anterior and posterior widths about equal (Allen, 1891). Lowest mean coefficient of variation for features of the interparietal-supraoccipital region is 9.94 for least supraoccipital width (Baumgardner and Schmidly, 1981).

Compared with *D. ordii*, the condylar portion of the lower jaw of mainland *D. compactus* is more depressed. The condyle of the latter is longer and different in form from that of *D. ordii*, having a broader angle with its plane being less oblique to the vertical plane of the ramus (Allen, 1891).

The fourth upper premolar exhibits the least molarization of the species of kangaroo rats examined by Dalquest and Carpenter (1986). The enamel pattern of relatively unworn fourth upper premolars is complicated and distinctive. The entostyle is large, anteriorly directed, and well separated from the hypocone. The metacone is elongated, extends anterolabially as an enamel wall, and bends abruptly anterolingually. The protocone curves lingually and posteriorly. The central valley opens broadly on the lingual side of this tooth and turns to circle the inner curves of the protocone and entostyle, nearly meeting the enamel of the outer curves of these cusps. This forms a bifurcated central valley, which is restricted to the lingual side of this tooth (Dalquest and Carpenter, 1986). The fourth lower premolar is quadrate (Wood, 1935). The anterior loph of upper molar one is widest of the upper series of molars with the crest of each successive tooth being smaller. The posterior lophes of this series are shorter than the anterior lophs (Wood, 1935). In adult *D. compactus*, the upper and lower teeth are rooted (Hibbard, 1954). This condition is referred to as non-evergrowing or Kleistodont (closed tooth) and is restricted to the premolars and molars (Nader, 1966). All specimens examined by Wood (1935) lacked grooves and concurrent enamel thinning on the sides of the cheek teeth. In occlusal view, the enamel of worn teeth of these specimens



FIG. 3. Dorsal, ventral, and lateral views of skull and lateral view of lower jaw of a male *Dipodomys compactus sennetti* (Texas Cooperative Wildlife Collection 29076) from Jim Hogg County, Texas. Photograph by T. H. Henry.

formed an unbroken ring surrounding a lake of dentine, thus, differing from most post Tertiary species of *Dipodomys* (Wood, 1935). Similar incidence of such features has been reported for specimens of some populations (Mustang Island, Hall, 1951; Mustang and Padre islands, Setzer, 1949); but other populations have various degrees of lingual and labial incompleteness of the external enamel border (Padre Island and Tamaulipas, Hall, 1951; island and mainland samples, Hibbard, 1954). Degree of lingual and labial dentine grooving and resultant occlusal breaks in cheek teeth is considered to be age-related and to occur later in life in *D. compactus* than in *D. o. richardsoni* (Hibbard, 1954).

The distal end of the bacula of *D. c. compactus* is strongly curved at a right angle to the shaft with variation occurring in the length of the resulting hook. The distal tip is essentially spatulate, flaring in a lateral plane, perpendicular to the dorsoventral plane

formed by the shaft and hook. The outer side of the tip is essentially flat. Some specimens exhibit a faint furrow dividing the proximal end of the baculum and the side of the tip toward the shaft (Jannett, 1976). Means (in mm) of bacular length, width, and height were 9.75, 1.40, and 1.90, respectively (Best and Schnell, 1974), for specimens of *D. c. compactus*. With the data of Best and Schnell (1974), Jannett (1976) calculated roundness of base (dorsalventral/lateral diameter) and index of robustness [(dorsalventral diameter of base + lateral diameter of base) X 100/length of baculum] values of 1.36 and 33.8, respectively. From freshly caught specimens, Jannett (1976) reported values (in mm) of 10.21, 0.87, 1.90, and 1.61 for length of baculum, dorsalventral diameter at midshaft, dorsalventral diameter of base, and lateral diameter of base, respectively. Roundness of base was calculated to be 1.18 and index of robustness was 34.4. Size ranges of the spatulate tip (in mm) were 0.26–0.35 for minimal lateral diameter and 0.32–0.53 for maximal width (Jannett, 1976). Although length approached significant difference, no statistically significant age variation in bacular measurements was noted between adults sacrificed at capture and adults held in captivity for 1–2 years (Jannett, 1976). Based on bacula, island *D. compactus* were placed in a subgroup of the genus *Dipodomys* containing *D. agilis*, *D. elephantinus*, *D. microps*, *D. peninsulae*, and *D. venustus* (Best and Schnell, 1974).

ECOLOGY. *Dipodomys compactus* inhabits sparsely vegetated areas with sandy soils throughout its range (Baumgardner and Schmidly, 1985). Although sometimes found on level soil, *D. c. compactus* usually is confined to dune areas and is always on the side away from prevailing winds (Bailey, 1905). They were reported in association with various plants including *Uniola paniculata*, *Andropogon*, *Monanthocloa*, *Croton*, *Helianthus* (Blair, 1952), and *Fimbristylis* (Selander et al., 1962). Mammals reported in association with kangaroo rats on selected islands are as follows: Mustang Island—*Spermophilus spilosoma*, *Geomys personatus*, *Onychomys leucogaster*, *Taxidea taxus* (Baker and Lay, 1938; Blair, 1952), *Reithrodontomys fulvescens*, *Sigmodon hispidus*, *Mus musculus*, and *Canis latrans* (Blair, 1952); Tamaulipan islands—*S. spilosoma*, *S. hispidus*, *Lepus californicus*, *C. latrans* (Hall, 1951), *Dasyurus novemcinctus*, *G. personatus*, *Perognathus flavus*, *Neotoma micropus*, *Procyon lotor*, *T. taxus*, *Canis* sp., and *Odocoileus virginianus* (Selander et al., 1962).

Collecting sites for *D. c. sennetti* had loose, deep sand (Blair, 1952). The Hebbronville, Texas site was a much overgrazed mesquite (*Prosopis* sp.) savanna. Vegetation consisted of the grasses *Aristida glauca*, *Bouteloua hirsuta*, *Chloris cucullata*, and, where mesquite had been cleared, abundant prickly pear (*Opuntia*). Associated mammals were *S. spilosoma*, *G. personatus*, *P. flavus*, *Chaetodipus hispidus*, *Peromyscus leucopus*, *O. leucogaster*, *N. micropus*, and *C. latrans*. Near Lytle, Texas, *D. compactus* was taken in an area cleared of native brush that was subsequently revegetated by *Aristida*, *Bouteloua*, *Andropogon*, and various herbaceous weeds. Other mammals obtained here were *Scalopus aquaticus*, *Geomys bursarius*, *P. flavus*, *C. hispidus*, *P. leucopus*, and *N. micropus* (Blair, 1952). *D. compactus* was abundant in the yellow-sand prairie of southeastern-mainland Texas (Bailey, 1905) and a kangaroo rat (probably referable to *D. c. sennetti*; Bailey, 1905) was common in the sandy, black-oak (*Quercus velutina*) region south of the Medina River in Bexar County where its burrows seemed most numerous in the poorest soil (Allen, 1896). A specimen from Gonzales County was recorded by Raun (1959) from an area of deep sandy soil supporting a post oak-blackjack oak association (*Quercus stellata*, *Q. marilandica*).

In areas of sympatry of *D. compactus* and *D. ordii*, these taxa exhibit microhabitat discrimination (Baumgardner and Schmidly, 1985). *D. compactus* was taken only on, or adjacent to, disturbed areas characterized by softer soil and lower, more open vegetation and was never captured on undisturbed brushland. *D. ordii* was taken primarily on undisturbed brushland and only rarely was associated with disturbed sites.

A specimen (probably referable to *D. c. sennetti*; Bailey, 1905) contained two small embryos on 23 August (Allen, 1896). One animal displayed two placental scars on 6 July and another had scrotal testes on 7 July (Selander et al., 1962).

Under laboratory conditions, *D. compactus* is strongly nocturnal. There is a mean activity outside its nest of <16% during lighted periods (Kennedy et al., 1973).

Of the 13 skulls of Tamaulipan specimens examined by Hall

(1951), two had parietal bones eroded by what seemed to be nematode worms. One of these skulls had the tympanic cavity perforated.

GENETICS. Of 18 loci examined by Johnson and Selander (1971), only transferrin was polymorphic in *D. c. compactus*. This subspecies had a mean number of alleles per locus per population of 1.03, a mean proportion of loci polymorphic per population of 0.03, and a mean proportion of loci heterozygous per individual of 0.023. Coefficients of genetic similarity among populations of this subspecies are high (0.98–1.00). Mean values between *D. c. compactus* and other kangaroo rats examined, ranged from 0.36 (*D. elator*) to 0.74 (*D. heermanni*); mean value between this race and *D. ordii* was 0.71. This biochemical evidence did not support earlier contentions that *D. compactus* was a subspecies of *D. ordii* (Davis, 1942; Setzer, 1949). *D. compactus* is genetically more distinctive from *D. ordii* than were any populations of *D. ordii* to each other. Cluster analysis of a matrix of Roger's coefficients grouped *D. compactus* with samples of *D. agilis*, *D. heermanni*, *D. microps*, *D. panamintinus*, and *D. spectabilis* (Johnson and Selander, 1971).

Karyotypic data for both subspecies are: $2n = 74$ (largest number of chromosomes in the genus; Stock, 1974); $fn = 144$; 4 metacentrics; 27 submetacentrics; 5 subtelocentrics; X chromosome is submetacentric; and Y chromosome is acrocentric-subtelocentric (Schmidly and Hendricks, 1976; Stock, 1974). To account for the karyotypic differentiation of *D. compactus* from *D. ordii*, Stock (1974) speculated that either the ancestral $2n$ of *D. ordii* was 74 and that a centric fusion occurred after Padre Island animals were isolated, but before *D. ordii* became widespread, or the island form originally had a $2n$ of 72 and that a centric fission occurred yielding an additional small pair of submetacentric chromosomes.

Dipodomys compactus has one of the highest levels of total nuclear deoxyribonucleic acid (DNA) content per nucleus reported for the genus (9.7 picograms; Hatch et al., 1976). With approximate values of 3.0 and 3.5 picograms per nucleus, this species has among the highest proportions of heavy satellite DNA (1.713 g/ml) and some of the smallest proportions of intermediate-density DNA (1.702 g/ml), respectively, for the genus (Hatch et al., 1976).

REMARKS. The taxonomic history of *D. compactus* has been much confused with that of *D. ordii*. Investigations examining relationships between these taxa have considered *D. compactus* to be either synonymous with *D. ordii* (Davis, 1942; Hall, 1981; Setzer, 1949; Stock, 1974) or a separate species (Baumgardner and Schmidly, 1981; Grinnell, 1921; Johnson and Selander, 1971; Schmidly and Hendricks, 1976). Despite an early report of *D. compactus* from the mainland of southern Texas (Thomas, 1888), most authorities have treated this species as occurring only on islands and in Tamaulipas, Mexico, and have considered all kangaroo rats on the southern Texas mainland referable to a single taxon (*D. ordii sennetti*). Because both *D. compactus* and *D. ordii* have extensively overlapping ranges on the mainland (Baumgardner and Schmidly, 1981), some researchers may have utilized samples containing both species or misidentified specimens. Such mixing of taxa could have confused patterns of variation and may have led to conclusions that kangaroo rats from the mainland of southern Texas were intermediate between island *D. compactus* and western Texas *D. ordii*. Information presented herein is for specimens considered *D. compactus* by Baumgardner and Schmidly (1981).

Dipodomys compactus was considered closely related to *D. ordii* in an interspecific analysis of external, cranial, and skeletal characters (Schnell et al., 1978). A similar conclusion was made in a study of external and cranial measurements (Best, in press).

I thank E. Anderson, S. Anderson, T. L. Best, M. L. Kennedy, and B. J. Verts for comments on an early version of the manuscript.

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